

SAMPLING CONSIDERATIONS FOR DEMOGRAPHIC AND HABITAT STUDIES OF NORTHERN GOSHAWKS

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ABSTRACT.—We used mark-recapture methods to monitor Northern Goshawks (*Accipiter gentilis*) and their nests over 12 yr in an increasing sample of breeding territories (37 in 1991 to 121 in 2002) in northern Arizona. As many as 8 yr of repeated nest searching were required to identify the population of breeders, as individuals skipped egg-laying on territories for up to 7 consecutive yr. Extensive temporal (within territory) and spatial (among territory) variation in reproduction and a high annual frequency of movements among dispersed alternate nests in territories made finding and monitoring goshawks problematic. Low detectability of nonbreeding goshawks (combined with uncertainties stemming from variations in breeding and use of alternate nests) made it difficult to categorize territories unequivocally as “unoccupied” by goshawks in non-egg-laying years. Temporal and spatial variation in reproduction required large numbers of territories to attain reliable estimates of reproduction of goshawks; such estimates were achieved only when samples approached or exceeded 60–100 territories. Our within-territory goshawk searching protocol, designed to increase the low and variable detectability of goshawks, required extensive sampling efforts to detect among-alternate nests movements. In lieu of such efforts, samples of territories occupied by goshawks may “decay” over time and lead to false inferences of population declines. Low detectability, variations in breeding, and large samples require that demographic and habitat studies of goshawks employ intensive and repeated searches for goshawks in large study areas over at least 8 yr.

KEY WORDS: Northern Goshawk; *Accipiter gentilis*; alternate nest; Arizona; bootstrap; detectability; monitoring; reproduction; sampling; territory occupancy.

CONSIDERACIONES SOBRE EL MUESTREO EN ESTUDIOS DEMOGRÁFICOS Y DE HÁBITAT DE *ACCIPITER GENTILIS*

RESUMEN.—Usamos técnicas de captura-recaptura para evaluar las actividades de *Accipiter gentilis* y de sus nidos a lo largo de 12 años en una muestra creciente de territorios de nidificación (37 en 1991 a 121 en 2002) en el norte de Arizona. Para poder identificar la población reproductiva de *Accipiter gentilis*, requerimos hasta 8 años de búsqueda repetida de nidos, ya que esta especie evitó poner huevos en territorios por períodos de hasta 7 años consecutivos. La gran variación temporal (dentro de los territorios) y espacial (entre territorios) en la reproducción y una alta frecuencia anual de movimientos entre nidos alternos dispersos en los territorios dificultó encontrar y evaluar las actividades de *A. gentilis*. La baja detectabilidad de los individuos no-reproductivos de *A. gentilis* (combinado con incertidumbres provenientes de las variaciones en la reproducción y en el uso alternativo de nidos) hizo difícil categorizar los territorios de modo inequívoco como “desocupados” por *A. gentilis* en los años en que no pusieron huevos. Esta dificultad se manifestó por la presencia de nidos activos de los mismos individuos anillados de *A. gentilis* luego de más de un año sin presencia reproductiva en los territorios. La variación temporal y espacial en la reproducción requirió grandes números de territorios para alcanzar estimaciones confiables de reproducción en *A. gentilis*. Estas estimaciones fueron obtenidas sólo cuando las muestras alcanzaron o excedieron los 60–100 territorios. Nuestro protocolo de búsqueda de *A. gentilis* dentro de los territorios, diseñado para incrementar la detectabilidad baja y variable de *A. gentilis*, requirió esfuerzos de muestreo amplios para detectar movimientos entre nidos alternos. Sin estos esfuerzos, las muestras de los territorios ocupados por *A. gentilis* podrían “disminuir” a lo largo del tiempo y llevarnos a inferencias falsas sobre disminuciones poblacionales. La baja detectabilidad, las variaciones reproductivas y la necesidad de muestras de gran tamaño requieren que los estudios demográficos y de hábitat

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de *A. gentilis* empleen búsquedas intensivas y repetidas de esta especie en grandes áreas de estudio durante al menos ocho años.

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The distribution, abundance, vital rates, and habitat occupancy of Northern Goshawks (*Accipiter gentilis*) are difficult to determine because of their elusive behavior in structurally-complex habitats, their low breeding densities, and annually variable breeding rates (DeStefano et al. 1994, Reynolds et al. 1994, Kennedy 1997, Reynolds and Joy in press). While locating and monitoring nests are common approaches in studies of avian demography and habitat, making valid inferences to a target population depends on reliable (unbiased and precise) estimates of the distribution and abundance of nests, demographic rates at nests, and habitat occupancy. In such studies, it is often too costly to detect all individuals and to sample all areas, making a census (complete count) impractical, especially in difficult-to-detect species. For such species, population parameters and habitat occupancy are often estimated using sampling methods. Making inferences about a species' distribution or habitat occupancy from samples requires inferences about the species' detection probability (probability that an individual is included in a sample when present). Biologists attempt to minimize influences of incomplete observations on estimates of a species' distribution, demographics, and habitats with sampling frameworks that increase the detection rates of the species (Peterson and Bayley 2004, McDonald 2004). The problem is to understand how detectability varies within and among individuals, both temporally (year-to-year) and spatially (among territories), and to develop sampling protocols and efforts that increase detection rates of all individuals.

We used mark-recapture methods from 1991–2002 to determine the distribution, abundance, vital rates, fidelity to mate and territory, natal and breeding dispersal, and habitat occupancy of goshawks breeding on territories that increased in number from 37 in 1991 to 121 in 2002 (Reynolds et al. 1994, Reich et al. 2004, Reynolds et al. 2004, Wiens 2004). Because these objectives required a census of breeding goshawks, we attempted to find all breeding goshawks in our study area. In this paper, we first describe the sampling protocols we used to initially locate and monitor breeding goshawks on the Kaibab Plateau. We then describe the

abundance and dispersion of breeding territories, the dispersion of alternate nests within territories, reproductive rates, and behaviors effecting goshawk detectability that resulted from 12 yr of implementing our protocols. Finally, we present bootstrap subsampling of our full samples of territories to estimate the number of breeding territories needed for precise estimates of the reproductive status and production of young by goshawks. Our purpose is to provide a framework for developing sampling protocols, sampling efforts, and sample sizes for demographic and habitat studies of goshawks in other populations.

STUDY AREA

The study area (1728 km²) was all of the Kaibab Plateau above 2182 m elevation above sea level, and contained ca. 122 400 ha of ponderosa pine (*Pinus ponderosa*) forests between 2075–2450 m elevation, ca. 51 600 ha of mixed-conifer forests between 2450–2650 m elevation, and ca. 30 600 ha of spruce (*Picea engelmannii*) fir (*Abies lasiocarpa*) forests between 2650–2800 m elevation (Rasmussen 1941, White and Vankat 1993). Pinyon (*Pinus edulis*) juniper (*Juniperus* spp.) woodlands occurred below the study area between 1830–2075 m elevation and shrub-steppe occurred below 1830 m. With the exception of several narrow (<1 km) meadows, several areas burned by wildfire, and numerous tree harvest areas, forests on the study area were contiguous (Reynolds et al. 1994, Joy et al. 2003). The southern one-third of the study area included the Grand Canyon National Park–North Rim (GCNP) and the northern two-thirds, the Kaibab National Forest (KNF). Forests on the Kaibab Plateau are isolated from other forests by varying distances of shrub-steppe; the nearest forest to the north, 97 km; to the east, 250 km; to the west, 80 km; and to the south, 89 km, with the exception of a small area of ponderosa pine forest on the south rim of the Grand Canyon at 18 km (Reynolds et al. 2004).

METHODS

Field Procedures. We defined a breeding territory as an area exclusively occupied by a pair of goshawks during a breeding season. This definition implied that territories were defended by resident goshawks, and the dispersion of breeding pairs was constrained by territoriality. While uncertain if or how territories were defended by goshawks, we estimated their size on the Kaibab Plateau as the area whose radius was half the mean distance among neighboring pairs. Recapture of marked goshawks showed that territorial owners, as well as their replacements over time, had strong life-time fidelity to their territory (Reynolds and Joy in press, R. Reynolds unpubl. data), and territories on the Kaibab Plateau appeared to be spatially fixed over years.

We located goshawk territories using two protocols: systematic foot-searches for goshawks and their nests in areas <1600 ha and broadcasts of goshawk vocalizations from stations on transects (Kennedy and Stahlecker 1993, Joy et al. 1994) in areas >2400 ha. Both nest-searching procedures were used each breeding season (April–August). A new territory was identified when a used goshawk nest (or, in rare cases, an occupied-only nest area; see below) was discovered in an area not already in a known territory and when the new nest (or nest area) was used by unbanded goshawks. Once a territory was found, it was added to that year's cohort of territories and assessed in all subsequent years for goshawk occupancy. Because we were unable to search our study area completely in a single year, we extended our nest searching into previously unsearched areas each year; hence, the number of territories under study increased over years. In addition to expanded nest searches, we annually re-searched areas (using both foot and broadcast searches) suspected of having territorial goshawks based on goshawk nest spacing (Reynolds and Wight 1978, Reynolds et al. 1994).

Goshawk territories often contain one or more alternate nests that are used by the goshawks over several years (Squires and Reynolds 1997, Reynolds and Joy in press). To prevent misclassifying the reproductive status of goshawks that may have moved to an alternate nest, we used a within-territory nest-searching protocol consisting of three sequential steps (Reynolds et al. 2004). Each year, beginning 3 wk before egg laying, we conducted "initial visits" to all known alternate nests and historical nest structures (existing nests with unknown histories of use) to determine if goshawks were present. Searches for goshawks, their feces, molted feathers, and nests refurbished with green twigs (Reynolds and Wight 1982) were conducted within 100-m radii of each alternate and historical nest. Initial visits to nests were completed in all territories by 2 wk after egg-laying. If a used nest in a territory was not found in an initial visit, a "foot search" was conducted within a 500-m radius circle centered on the last-used nest or the centroid of the territory (determined subsequent to discovery of >1 alternate nests in a territory). Territory centroids were the geometric means of coordinates of alternate nests weighted by the number of yr each alternate nest was used during our study (Reynolds et al. 2004, Reynolds and Joy in press). A foot search involved systematically walking the 500-m radius circle looking for goshawks or signs of their presence (see above). Foot searches were conducted from egg laying to about 15–20 d after egg-hatching. In territories where used nests were not located in foot searches, a "broadcast search" was conducted in a 1600-m radius circle centered on either the last-used nest or the territory centroid. Broadcasting of goshawk vocalizations were conducted from stations on transects arranged as described by Joy et al. (1994). Broadcast searches were conducted from about 10 d after egg hatching to the end of the post-fledging dependency period (late August or early September). All nest trees were mapped to the nearest 3 m with a global positioning system.

Nests were "used" if goshawks laid eggs, and territories were "occupied-only" if eggs were not laid but evidence (goshawks observed, molted feathers, feces, reconstruct-

ed nest) of goshawk presence was found in association with a nest structure, or "unknown" if insufficient evidence of occupancy was found. All used nests were visited weekly to count numbers of nestlings and fledglings and to determine the approximate timing and causes of nest failure. Goshawk nestlings were banded in the 10 d before fledgling, and numbers of nestlings present at the time of banding was considered the number of young produced. Nesting adults were captured with dho-gaza nets placed in nest areas and baited with live Great Horned Owls (*Bubo virginianus*) during the nestling period (Reynolds et al. 1994). All goshawks received a U.S. Geological Survey leg band and a colored-aluminum leg band with a unique alpha-numeric code readable from 80 m with 40–60× telescopes (Reynolds et al. 1994). Annual field efforts of crews consisting of 15–23 persons were focused on finding new territories, finding nests within known territories, and capturing and recapturing (or resighting) goshawks on the study area.

Data Analysis. We used Dirichlet tessellation and Delauney triangulation (Cressie 1991) to estimate the distances between the centroids of first-order neighboring goshawk territories. To estimate the dispersion of alternate nests within territories, we measured the within-territory map distances between each alternate nest (inter-alternate nest distance) and the within-territory centroid to each alternate nest (centroid-to-alternate nest distance; excludes territories with only one nest). To test for differences in the spacing of goshawk territories in the KNF and the GCNP, we used a two-sample *t*-test. To characterize the strength of the relationship between the numbers of new territories found in a year and the proportion of territories used in a year, we used a Spearman's correlation coefficient (r_s). The annual proportion of territories with used nests was calculated as the proportion of those territories under study in the previous year (prior-year's cohort of territories) that had used nests in the current year (Reynolds and Joy in press). We did this because the number of territories under study increased annually, and we included only territories that were monitored from before egg-laying to minimize bias associated with missed failed nests. We defined nest success as the proportion of used nests in a prior year's cohort of territories that produced ≥ 1 fledgling. To examine annual differences between the proportion of territories with used nests and the mean number of young produced per used nest, we calculated 95% Confidence Intervals (CI) for these parameters and visually assessed the degree of CI overlap among estimates.

We used the bootstrap method (Efron and Tibshirani 1993) to estimate the number of goshawk territories that needed monitoring to attain precise estimates of the proportion of territories with used nests, nesting success, and number of young fledged per used nest. Our objective was to display variability in these parameters for different-sized samples given the full sample estimate. We conducted, with replacement, 1000 bootstrap iterations with sample sizes of 20, 40, 60, 80, 100, and 120 territories. We present the bootstrap results in box and whisker plots for only 2000 and 2002 because numbers of territories under study during those years were similar (120 and 121), and 2000 was a relatively good breeding year (55% of territories had used nests), while 2002 was a relatively

Table 1. Total territories, number of used nests (eggs laid), and number and percent of territories from previous year's cohort of territories with used nests on the Kaibab Plateau, Arizona, 1991–2002. Previous-year's territory cohorts were used because all territories in that cohort were monitored from before egg-laying in a current year, minimizing bias created by missing used nests due to early nest failure.

	YEAR											
	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002
Total territories	37	64	82	88	99	105	106	109	113	120	120	121
Total used nests	36	59	67	21	53	46	31	58	57	66	30	21
Used nests in previous year's cohort		32	49	18	44	40	31	55	56	60	30	21
Percent used in cohort		86	77	22	50	40	30	52	51	53	25	17

poor breeding year (17% of territories had used nests). We plotted the medians of the estimates of the bootstrap subsampling for the proportions of territories with used nests and for nesting success. For mean young fledged per territory, we plotted the medians and coefficients of variation of the bootstrap estimates. We used a CV of 20% as a target criterion for identifying a level of sampling needed to attain adequate estimates of numbers of young per territory (see Pollock et al. 1990).

RESULTS

The Study Population. Numbers of goshawk territories under study increased from 37 in 1991 to 121 in 2002 as searches for new territories were annually extended into unsearched areas and as previously searched, but unoccupied areas, were searched again (Table 1). By 2002, about 95% of the KNF and 60% of the GCNP had been searched for nests. A total of 121 territories were discovered, and goshawks laid eggs in 1 or more years on all but six of these. Exceptions (two KNF, four GCNP territories) included territories occupied in ≥2 yr by goshawks that built new, or reconstructed old, nests but did not lay eggs during the study. Territory centroids were regularly spaced (Reich et al. 2004, Reynolds and Joy in press). The mean Delaunay triangle distance between 120 territory centroids (1 territory not included due to inadequate search for surrounding territories) was 3.8 km (SD = 1.3 km, min = 1.3 km, max = 8.1 km, N = 302 first-order neighbor distances; inter-centroid distances that crossed unsearched areas in the extreme southeast of the study area were not included; Fig. 1).

We estimated the total number of breeding territories on the study area by calculating an “exclusive” area for each pair of goshawks using one-half the mean distance between territory centroids (3.8

km) as the radius and dividing the study area (173 200 ha) by the exclusive area (1134 ha; Reynolds and Joy in press). This should result in an accurate estimate of the total number of territories because of the regular spacing of territories (known for 80% of our study area) and because forests on the study area were nearly contiguous (Reynolds and Joy in press). The study area was large enough for there to be approximately 150 territories, five territories more than our 1996 estimate (Reynolds and Joy in press). This increase reflected the discovery of 17 new territories between 1997 and 2002 and a subsequent 0.1 km reduction in the mean inter-centroid distance. Therefore, our sample of 121 known territories represented about 80% of the potential total number of goshawk territories in our study area.

Temporal and spatial variation in the frequency of egg-laying by goshawks on the study area was extensive. Temporal variation reflected periods of years with increasing or decreasing proportions of goshawks that laid eggs (Table 1, Fig. 2), and spatial variation reflected differences in the frequencies of egg-laying among territories (Table 2). In the 12 yr during which the 37 territories in the 1991 cohort were monitored, 13 territories (36%) had used nests in ≤6 yr and 23 (64%) had used nests in ≥7 yr (1 territory never had a used nest), and of the 27 new territories found in 1992, 17 (63%) had used nests in ≤5 yr and 10 (37%) had eggs in ≥6 of the 11 yr they were monitored (Table 2). Overall, 75% (86 of 115 territories that had used nests in ≥1 yr) of territories had used nests in ≥3 yr. Most (87%) territories in which egg laying was skipped in ≥1 yr had used nests or were occupied-only in subsequent years, often by the

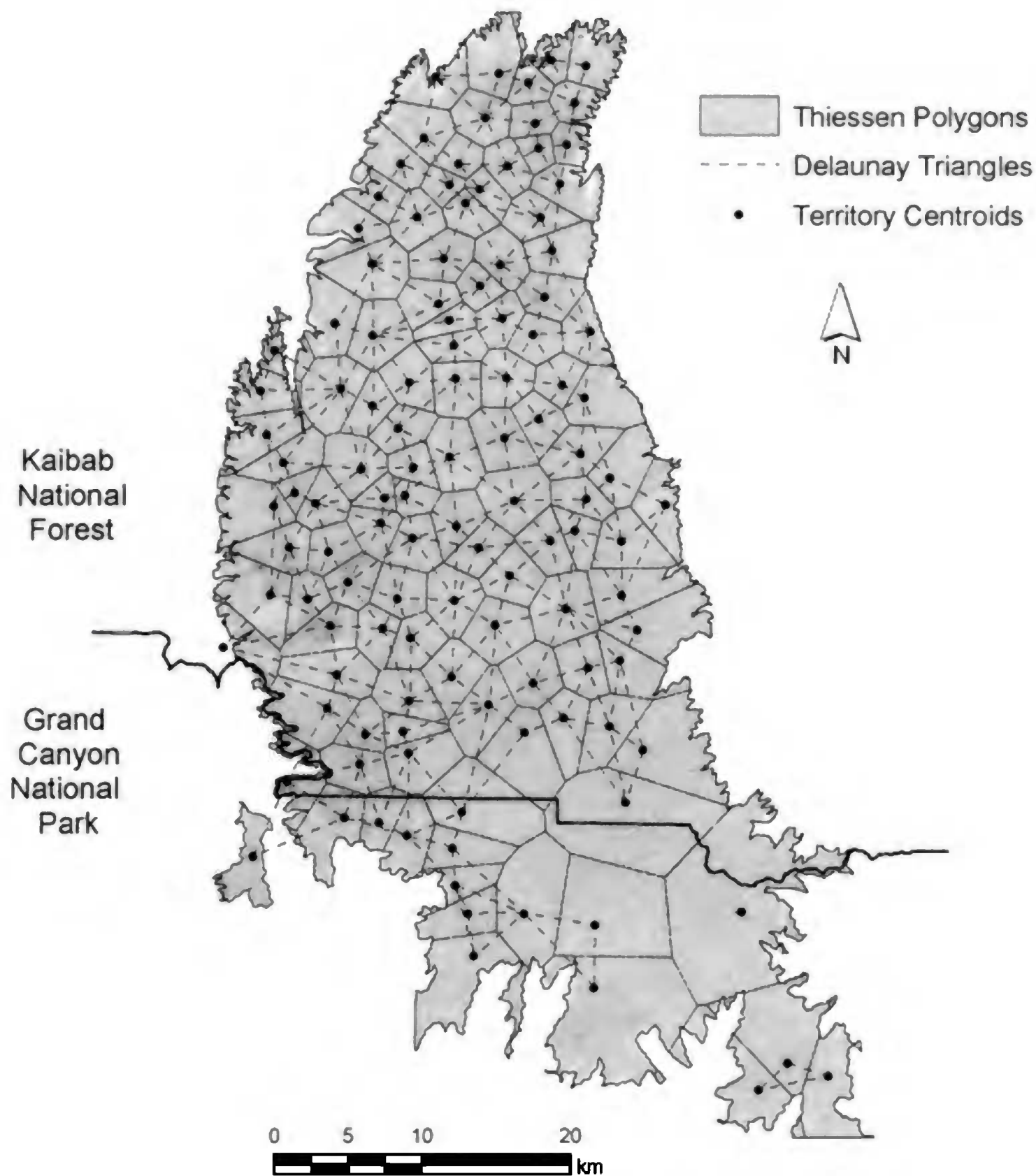


Figure 1. Thiessen polygons and Delaunay triangles used to calculate first-order nearest neighbor distances between Northern Goshawk territory centroids on the Kaibab Plateau, Arizona, 1991–2002 ($N = 120$, see text). Mean inter-centroid distance was 3.8 km ($SD = 1.3$ km, $min = 1.3$ km, $max = 8.2$ km, $N = 302$ triangle legs).

same banded goshawks that had previously laid eggs on the territory (R. Reynolds unpubl. data).

Of a combined total of 435 used nests in all 11 prior-year cohorts of territories, 341 (63%) were successful (Table 3). Of 94 nest failures, 59 (63%) failed during the incubation period, and 35 (37%) failed during the nestling period. There was minimal among-year variation in nesting success (Table 3, Fig. 2). In 459 broods (not limited to nests in

prior-year cohorts) with accurate counts of young, brood sizes ranged from 1–4 nestlings (median = 2; Table 2); 102 (22%) broods had one young, 219 (48%) had two young, 133 (29%) had three young, and five (1%) had four young. The mean annual number of fledglings produced per used nest was only moderately variable compared to the annual variation in the proportion of territories with used nests; the CV of the number of young produced

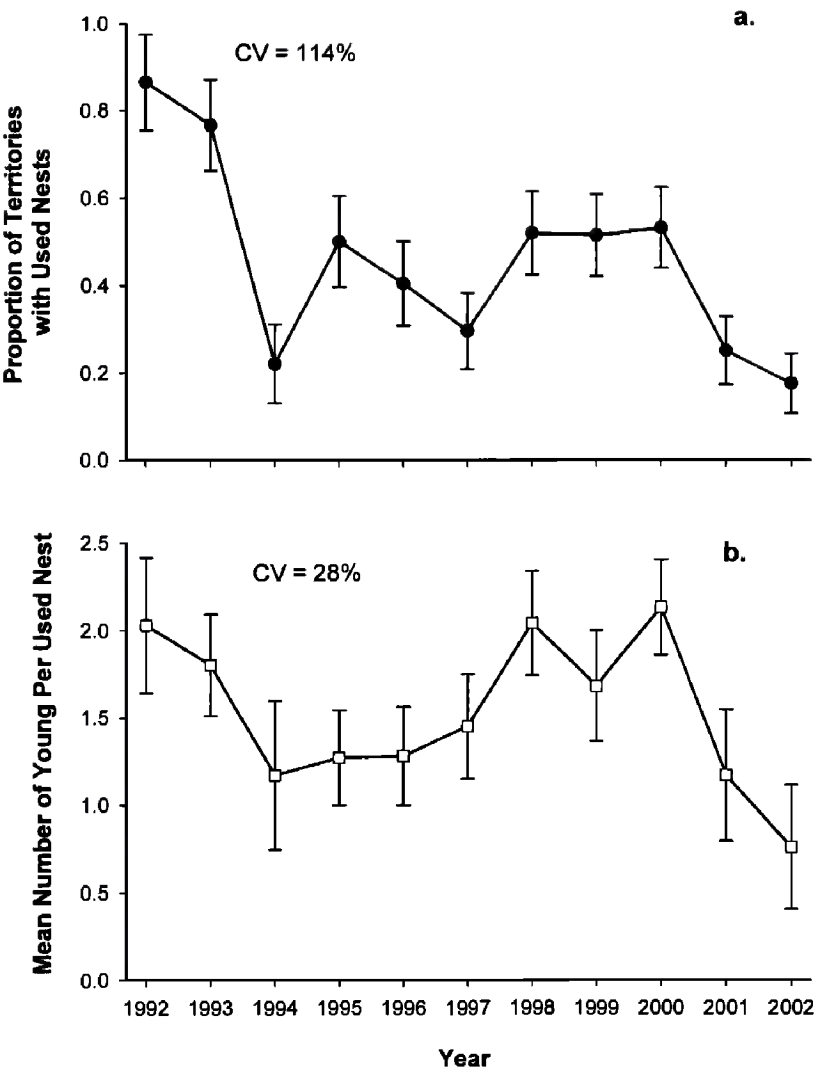


Figure 2. Annual variation in (a) the proportion of territories under study containing active (eggs laid) Northern Goshawk nests and (b) in the mean numbers of young produced per used nest in the previous year's cohort of goshawk nests (see text) on the Kaibab Plateau, Arizona, 1991–2002. Error bars represent $\pm 95\%$ CI.

per used nest was 28%, while the CV of the proportion of territories with used nests was 114% (Fig. 2). Likewise, the among-year variation in total young produced by the 1991 cohort of territories ($N = 37$) over 12 yr was also higher than the among-year variation of the means of young produced per used nest for the same territories and years. Total young produced ranged from 16 in 2002 to 65 in 1992 and had an among-year coefficient of variation (CV) of 68%, and mean number of young produced per used nest ranged from 0.6 in 2002 to 2.4 in 2000 and had a CV of 37%. Thus, both the annual proportion of territories with used nests and total young produced per year provide a more sensitive measure of the variable reproductive output of goshawks than the annual mean number of young produced per used nest.

Goshawk Behavior and Sources of Error. How well an estimate represents the true spatial distribution, density, or habitat occupancy of a species

Table 2. Number and percent of new Northern Goshawk territories discovered each year of the study and the numbers of years the new nests were used (eggs laid) in subsequent years on the Kaibab Plateau, Arizona, 1991–1996.

NEW TERRITORIES FOUND	NUMBER (%) OF YEARS WITH USED (EGGS LAID) NEST											
	1	2	3	4	5	6	7	8	9	10	11	12
1991	36 ^b	2 (6)	3 (8)	6 (17)	—	2 (6)	5 (14)	7 (19)	8 (22)	2 (6)	1 (3)	—
1992	27	—	5 (19)	4 (15)	6 (22)	2 (7)	4 (15)	3 (11)	1 (4)	—	1 (4)	—
1993	18	4 (22)	2 (11)	1 (6)	5 (28)	2 (11)	1 (6)	3 (17)	—	—	—	—
1994	6	1 (17)	—	—	—	2 (33)	3 (50)	—	—	—	—	—
1995	11	3 (28)	1 (9)	2 (18)	—	3 (28)	1 (9)	—	1 (9)	—	—	—
1996	6	1 (17)	2 (33)	—	3 (50)	—	—	—	—	—	—	—

^a 1997–2002 not displayed because too few years of monitoring were available.

^b One territory was occupied by goshawks who never laid eggs.

Table 3. Number of used (eggs laid) and successful (fledged ≥ 1 young) nests, mean and standard deviation (SD) of fledglings per used nest, and proportion of used nests within the prior year's cohort of Northern Goshawk territories that fledged young on the Kaibab Plateau, Arizona, 1991–2002.

	YEAR										
	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002
Used nests	32	49	18	44	40	30	55	56	60	30	21
Fledglings/ used nest	2.0	1.8	1.1	1.3	1.3	1.5	2.0	1.7	2.1	1.2	0.8
SD	1.12	1.04	0.92	0.92	0.91	0.85	1.13	1.21	1.08	1.05	0.83
Successful nests	26	42	13	34	31	25	46	41	53	19	11
Percent nests successful	81	86	72	77	78	83	84	73	88	63	52

depends on the error associated with the estimate (Thompson et al. 1998). A potential source of sampling variation is an incomplete count of breeding goshawks. Counts are related to the actual size of the territorial goshawk population by the probability of detection, which may vary systematically. Because of their defensive behavior at nests, the detectability of breeding goshawks (still relatively low due to their elusiveness and complex habitats) is much higher than the detectability of non-nesting goshawks (including those whose nests failed). Low detectability of nonbreeders combined with the large annual variation in numbers of goshawks breeding can produce large sampling variation. To account for the low detectability of nonbreeders, we repeatedly searched areas suspected of containing goshawks. Eleven yr of repeated searching for nests showed that the KNF was nearly saturated with breeding territories (Fig. 1). We do not know if the GCNP was similarly saturated with territories because only ca. 60% of the GCNP was searched for goshawks. However, the mean distance between centroids of known territories in the GCNP was not significantly different from the mean distance between KNF centroids (KNF \bar{x} = 3722 m, SD = 1221 m, N = 271 triangle legs; GCNP \bar{x} = 4028 m, SD = 1477 m, N = 22 triangle legs; t = -1.1, df = 291, P = 0.27), suggesting that the density of goshawk territories in the GCNP was similar to territory density in the KNF. The success of finding new territories in a year was positively related to the proportion of territories with used nests in that year (r_s = 0.73, P = 0.011, N = 11); we found more new territories in good breeding years (1991–93, 1998–2000) than in poor breeding years (1994, 2002).

Another source of measurement error is misclassification of the breeding status of territorial goshawks. Detecting movements of goshawks among alternate nests required considerable sampling effort, the level of which depends on the number and distribution of alternates within territories and frequency of movement among the alternates. Because numbers of known alternates depends on years of monitoring, we only report the numbers of alternate nests in the 1991 and 1992 cohorts of territories. Mean number of alternates in these territories was 3.2 (SD = 1.5 nests, min = 1, max = 6, N = 36) and 2.9 (SD = 1.4 nests, min = 1, max = 6, N = 27), respectively. The frequency distribution of inter-alternate nest distances within all territories with ≥ 2 alternates (N = 91 territo-

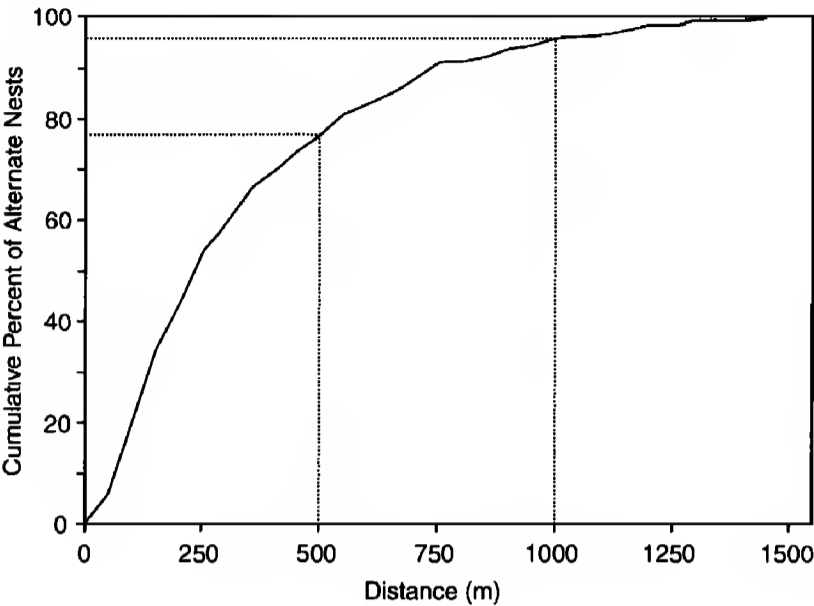


Figure 3. Cumulative percent of alternate nests within territories with increasing distance (m) between territory centroids to alternate nests on the Kaibab Plateau, Arizona. Maximum centroid-to-alternate nest distance was 1452 m.

ries) was right-skewed with a median of 402 m (\bar{x} = 612 m, SD = 569 m, min = 9 m, max = 2426 m, N = 308 alternate nests). When measured from territory centroids, the median centroid-to-alternate distance was 228 m (\bar{x} = 334 m, SD = 298 m, min = 6 m, max = 1452 m, N = 273 alternates in 91 territories), about half of the median inter-alternate nest distance. The cumulative proportion of alternates captured with distance from centroids showed that about 75% occurred within 0.5 km, and about 95% occurred within 1 km of centroids (Fig. 3). Thus, our territory-focused broadcast

searching protocol in areas of 1.6-km radius around centroids exceeded the maximum known centroid-to-alternate distance (1452 m). The frequency of movement of egg-laying goshawks to alternates was high; an annual mean of 64% of breeding goshawks moved to an alternate, and 42% of these movements were to new (unknown to us) alternates (Table 4).

Sample Size. Bootstrap subsampling showed that samples of ca. 60–80 territories in good breeding years and 80–100 territories in poor breeding years were needed for precise estimates of the full sample means of the proportion of territories with used nests and nesting success on the Kaibab Plateau (Fig. 4). Coefficient of Variation plots of the mean young per used nest in good breeding years showed that subsamples of ≥ 80 territories had bootstrap estimates entirely below a CV of 20%, although many of the estimates from subsamples of 60 territories were below 20% (Fig. 5). In poor breeding years, subsamples of 100 territories were insufficient to achieve a CV of less than 20%, reflecting the few (21) territories that were occupied in 2002. How temporal and spatial variation in reproduction on the Kaibab Plateau compares to other goshawk populations is unknown because other studies typically reported reproduction at only used or successful nests (e.g., Reynolds and Wight 1978, DeStefano et al. 1994, Doyle and Smith 1994, Younk and Bechard 1994); only Keane et al. (in press) and Reynolds and Joy (in press)

Table 4. Number (%) of breeding Northern Goshawks that stayed in the previous year’s nest or moved to a new or previously-used alternate nest within their territory on the Kaibab Plateau, Arizona, 1991–2002.

YEAR	MOVEMENT			TOTAL PERCENT MOVING
	STAYED	TO NEW ALTERNATE	TO PRIOR ALTERNATE	
1992	14 (45)	17 (55)	—	55
1993	17 (35)	26 (53)	6 (12)	65
1994	7 (39)	7 (39)	4 (22)	61
1995	18 (43)	17 (40)	7 (17)	57
1996	9 (24)	16 (43)	12 (32)	76
1997	9 (30)	14 (47)	7 (23)	70
1998	19 (35)	27 (50)	8 (15)	65
1999	21 (38)	18 (32)	17 (30)	63
2000	18 (30)	20 (33)	22 (37)	70
2001	13 (43)	10 (33)	7 (23)	57
2002	7 (33)	8 (38)	6 (29)	67
Total	152 (36)	180 (42)	96 (22)	64

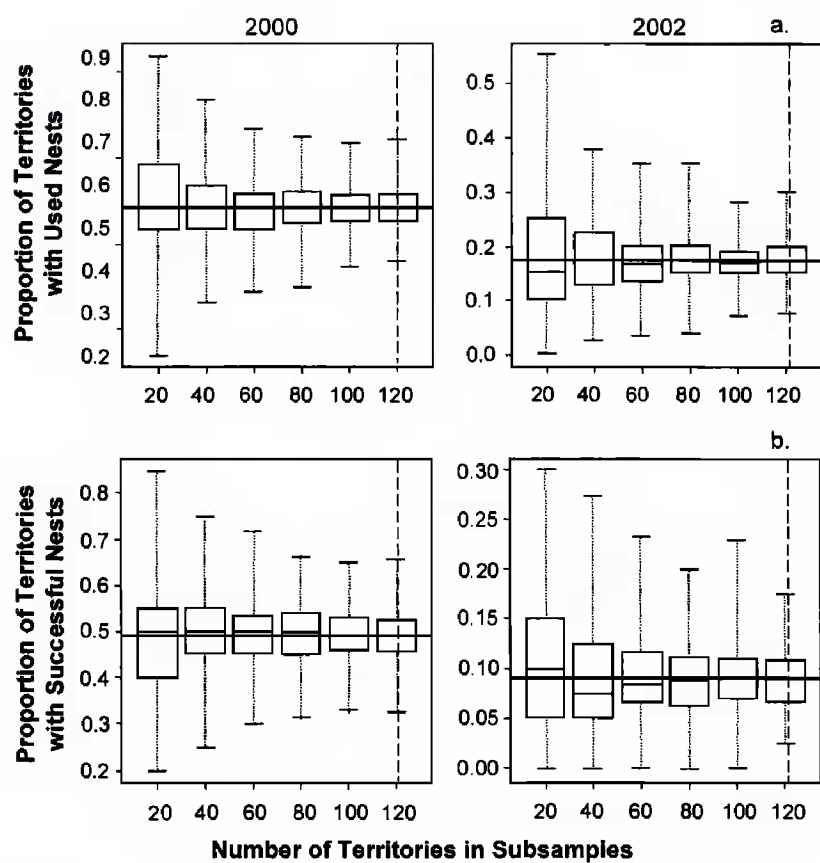


Figure 4. Box plots of bootstrap subsamples estimating the effects of sample size in good (2000) and poor (2002) breeding years on estimates of the proportion of Northern Goshawk territories with used nests (eggs laid) (a) and nesting success (b) on the Kaibab Plateau, Arizona, 1991–2002. Dotted vertical lines are numbers of territories (120 in 2000, 121 in 2002) used to estimate the true sample means (solid horizontal lines). Box plot whiskers extend to the maximum and minimum estimates, boxes represent the first and third quartiles of estimates, and the horizontal lines within boxes represent the medians of estimates.

reported the extent of temporal variation in the proportion of pairs breeding.

DISCUSSION

Goshawk populations are difficult to enumerate and monitor because of their elusive behavior, relatively low densities, and their structurally-complex forest habitats. Nonetheless, goshawk detectability increases during breeding (a 6-mo period) because of their aggressive nest defense. However, detectability of goshawks was highly variable among individuals because of extensive temporal (year-to-year) and spatial (among territory) variation in breeding. Within a year, nonbreeding territorial individuals have lower detectability than breeders, and among years, low-quality individuals (Wiens and Reynolds 2005) or individuals on low-quality territories have lower detectabilities than higher-quality individuals or those on higher-quality territories because they breed less often. Detectability

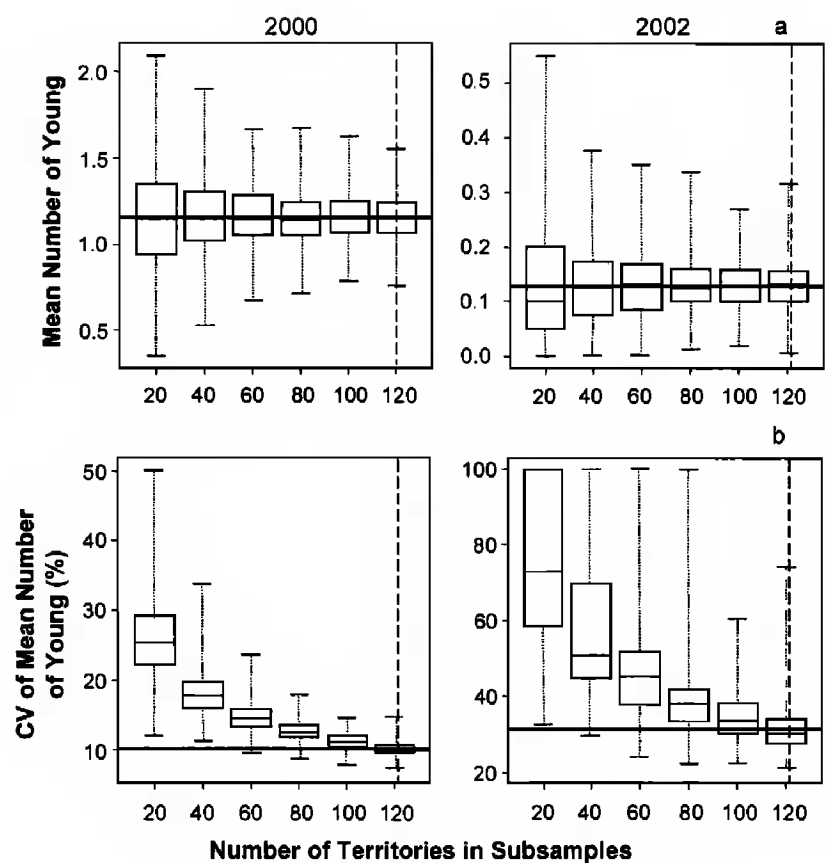


Figure 5. Box plots of bootstrap subsamples estimating the effects of sample size in good (2000) and poor (2002) breeding years on estimates of (a) the mean, and (b) the coefficient of variation (CV), of young produced per used (eggs laid) Northern Goshawk nest on the Kaibab Plateau, Arizona, 1991–2002. Dotted vertical lines are numbers of territories (120 in 2000, 121 in 2002) used to estimate the true sample means (solid horizontal lines). Box plot whiskers extend to the maximum and minimum estimates, boxes represent the first and third quartiles of estimates, and the horizontal lines within boxes represent the medians of estimates.

within and among individuals can also be variable from year-to-year because of the number and dispersion of alternate nests, and the frequency of movement among them. Finally, breeders whose nests fail have lower detectability than successful breeders. Therefore, determining the distribution, abundance, and habitat of a population of territorial goshawks and their annual breeding status requires sampling protocols and efforts that provide for the detection of both breeding and nonbreeding goshawks. Repeated nest searching of areas suspected of having breeding goshawks (“holes” based on territory spacing) eventually showed that our study area was saturated with breeding territories. Repeated searching was required because as many as 8 yr elapsed on some territories between egg-laying. Not surprisingly, our success in locating territories depended on the quality of the breeding year; more new territories

were found in years when larger proportions of goshawks laid eggs.

Nest searching did not cease with the discovery of a territory. Annually, between 50–75% of egg-laying goshawks moved to alternate nests within their territories, and in some years, more than half of these moves were to alternates unknown to us, some of which were more than 1.4 km apart. Such movements have long been recognized as making the monitoring of breeding goshawks difficult (Woodbridge and Detrich 1994, Reynolds et al. 1994, Kennedy 1997). In attempts to locate goshawks that may have changed nests, Kennedy (1997) and Woodbridge and Detrich (1994) searched 0.7–1.0 km and 1.6 km around the previously-used nest in a territory, respectively. If the distribution of alternates within territories on the Kaibab Plateau is representative of the distribution of alternates elsewhere, then these radii would contain 95 and 100% of alternate nests, respectively, but only if the nest last used was close to the center of the territory. However, the farther the last-used nest was from the center of a territory, the higher the probability of missing alternates with these radii. This suggests that in the early years of a monitoring study, longer search radii should be used, at least until centroids of territories can be estimated.

In studies of goshawk demography (e.g., Reynolds and Wight 1978, DeStefano et al. 1994, Reynolds et al. 1994, Kennedy 1997, Reynolds and Joy in press) and habitat (e.g., Bosakowski et al. 1999, Daw and DeStefano 2001, Finn et al. 2002, Joy 2002, McGrath et al. 2003, La Sorte et al. 2004), valid inferences to the target population depend on an adequate temporal and spatial sampling. Our study showed that, because breeding is temporally and spatially variable and the detectability of nonbreeders is low, accurate estimates of the number and location of nests and territories depends on constancy in annual sampling efforts and numbers of years over which surveys are conducted. Insufficient sampling for territories results in underestimates of breeding densities and habitat occupancy, and insufficient searches for nests within territories results in underestimates of annual proportions of pairs breeding and production of young. Because of large variation in the frequency of breeding, high rates of movement among nests, and low detectability of nonbreeders, it is particularly difficult to demonstrate unequivocally that territories are unoccupied in a year in which a used

nest is not found. These factors, especially when combined with insufficient sampling, may result in an apparent decrease in territory occupancy and, ultimately, a population decline. The difficulty of confirming that a territory is actually unoccupied is the basis for our assigning territories with insufficient evidence of occupancy as “unknown.” That territories continue to be occupied during non-breeding years was demonstrated by the fact that in many cases, the same color-marked goshawks were found to nest on the same territory before and after up to a 7 yr break in egg-laying (R. Reynolds unpubl. data). Because of this, we suggest that “territory occupancy rate” (proportion of known territories occupied), a commonly used reproductive parameter for goshawks (Crocker-Bedford 1990, Kennedy 1997), may be a biased estimator of the number of breeders in a population. Finally, the frequency of movements among alternate nests suggests that the scale of measurement for determining the breeding status and reproduction of goshawks should be at the territory level and not at the nest area.

An objective of population monitoring is to obtain reliable estimates from samples to infer changes in a target population. Our bootstrapping results showed that large samples of territorial goshawks (often larger than attained in many goshawk studies) were needed for precise estimates of the proportion of territorial goshawks breeding and their nesting success and reproduction. Large samples are needed because of the extensive annual variation in the proportion of territories with reproductive goshawks. Whether equally large samples of territories or pairs of goshawks are needed for reliable estimates of these parameters in other populations will likely depend on whether these populations are as temporally and spatially variable in reproduction as the Kaibab Plateau population. DeStefano et al. (1994) in Oregon, Doyle and Smith (1994) in northwestern Canada, Woodbridge and Detrich (1994) in northern California, Kennedy (1997) in New Mexico, and Keane et al. (in press) in central California, all reported moderate to extensive temporal variation in goshawk reproduction. Both the proportion of territories with egg-laying goshawks and total young produced on the Kaibab Plateau were more variable among years than mean numbers of young produced per used nest per year, the most commonly reported goshawk reproductive parameter (Kennedy 1997 and references therein). Because the proportions

of goshawks breeding and total young produced in a year more accurately portrayed the extent of annual variation in reproduction of the Kaibab goshawk population, both are likely to better describe a population's response to fluctuations in resources (e.g., food abundance; Salafsky 2004, Salafsky et al. 2005) and habitat quality than numbers of young produced per used nest.

CONCLUSION

Stratification of a study area, protocols for detecting species, and sampling efforts in studies are based on subjective and previous information (Morrison et al. 2001). Our nearly complete census of breeding goshawks on the Kaibab Plateau provides information on the distribution, density, variation in reproduction, and breeding behavior of territorial goshawks in one population. Our intent in presenting these data was to provide a framework for developing sampling protocols and identifying sampling efforts that may be needed to reliably estimate the distribution, density, vital rates, and habitats of breeding goshawks in other populations. Extensive temporal and spatial variation in reproduction on the Kaibab Plateau required as many as 8 yr of repeated nest searching to identify a population of breeders and annual searches of areas of 1.4-km radius around territory centers for reliable estimates of the reproductive status of territorial pairs. Further, as many as 60–80 goshawk territories were needed for precise estimates of the annual production of young by a population. The specific sampling protocols and efforts used in our study, and the samples of territories identified in this paper, demonstrate that demography and habitat studies of goshawks may have to employ intensive and repeated searches for goshawks in large study areas over at least 8 yr.

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